Temporal dynamics and causes of postharvest mortality in a selection-managed tolerant hardwood forest

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A B S T R A C T

Tree mortality following partial harvesting may significantly affect tree community dynamics, timber supply, and wildlife habitat in managed forests. However, the rates, causes, and consequences of postharvest mortality (PHM) have rarely been investigated in commonly used silvicultural systems. We applied a chronosequence approach combined with tree-ring-based dating of mortality events to investigate PHM following single-tree selection silviculture in a hardwood forest in central Ontario, Canada. Observed rates of PHM were best described by a negative exponential model, with an initial peak of 0.78–0.94% year^{-1} occurring within the first two years postharvest, and decreasing to ~0.55% year^{-1} three through five years postharvest. At six through 10 years postharvest, observed tree mortality was stable at ~0.21% year^{-1}: these rates were considerably lower than those observed in unmanaged stands at the same site (0.96% year^{-1}). Trees $\leqslant$17 cm in diameter were most susceptible to PHM, as were two softwood species (*Picea glauca* (Moench) Voss and *Abies balsamea* (L.) Mill.) and *Betula alleghaniensis* Brit. *Acer saccharum* Marsh. and *Fagus grandifolia* Ehrh. were least susceptible. Causes and types of mortality changed significantly with time after harvest: initially, mechanical damage from skidding and felling resulted in most dead trees observed as downed wood. With time, biotic agents (fungal infections, senescence) became more prevalent agents of mortality, increasing the proportions of standing dead trees. Our results indicate that PHM rates following selection harvesting are small compared to those following other retention harvest systems, but in the long term disproportionate effects on certain species are likely to affect the structure and function of managed northern hardwood forests.

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1. Introduction

In much of the northern hardwood forest region of North America, selection silviculture is a common forest management system and it is progressively becoming a more common forest management practice globally. In single-tree selection harvests in eastern North America, roughly 30% of standing basal area is removed from the stand and residual trees are retained across a full range of size classes approximating a target tree diameter distribution, intended to ensure recruitment of trees into successively larger size classes (Nyland, 1998). Also retained are other critical habitat features such as large live trees, a continuous canopy with multi-layered vegetation, substantial coarse woody debris, and both cavity and mast trees (Coates and Burton, 1997; OMNR, 1998; Franklin et al., 2002). Since a relatively small proportion of trees are removed in a given stand entry, selection silviculture is often considered more ecologically benign than other silvicultural systems (Caspersen, 2006).

With single-tree selection harvesting, a large proportion of the residual trees are exposed to possible mechanical damage during felling and skidding operations (Lamson et al., 1985; Ostrofsky et al., 1986; Cline et al., 1991; Anderson, 1994; Nichols et al., 1994). While damage following selection harvests has been well documented, understanding and quantifying how the damage may affect stand structure and dynamics remains largely speculative (e.g. Moore et al., 2002). A few studies have evaluated how harvest-related damage influences residual wood quality and/or postharvest growth rates (Nyland et al., 1977; Cline et al., 1991; Hartmann et al., 2008; Jones et al., 2009). By comparison, the effects of selection harvests on postharvest tree mortality (PHM) have not been well documented.

Following partial or structural retention harvests (*sensu* Groot et al., 2005), the rate of PHM has been suggested as one of several possible means to objectively assess the success or failure of silvicultural treatments. For example, based on an informal survey of British Columbian foresters, Coates (1997) suggested residual tree mortality rates >10% would be sufficient to deem a silvicultural treatment a "failure". From a timber management perspective, elevated PHM can drastically influence timber supply projections,

and has been shown to strongly affect stand structure and long-term dynamics, at least in boreal forests (e.g. Thorpe et al., 2010). From an ecological perspective, the effects of elevated PHM rates in managed hardwood forests are less clear. Some authors have suggested higher tree mortality may be beneficial as it creates high-value wildlife habitat in the form of coarse woody debris (Thorpe and Thomas, 2007; Vanderwel et al., 2008, 2010); others have found that selection harvests can either reduce or increase the amount of wildlife habitat such as standing dead trees (snags) and live cavity trees (Holloway et al., 2007; Kenefic and Nyland, 2007; Bladon et al., 2008; Cimon-Morin et al., 2010). Quantifying PHM is thus critical both from ecological and management perspectives to evaluate how silvicultural treatments influence forest structure and function.

To date most research on PHM in North America has been concentrated in boreal or western conifer forests, where retention rates are much lower than those following selection harvests (reviewed by Thorpe and Thomas, 2007; Bladon et al., 2008; Thorpe et al., 2008; Cimon-Morin et al., 2010; Spence and MacLean, 2011; Solarik et al., 2012). These studies indicate that postharvest mortality rates are highly variable, ranging between very small increases of <2% (e.g. Coates, 1997; Deal et al., 2002) to considerable increases of over 75% (Ruel et al., 2001). By comparison, few published studies have quantified mortality rates after single-tree selection harvesting. Caspersen (2006) found that, compared to background mortality rates (1.5% year^{-1}), tree felling increased tree mortality by 0.2–3.3%; these elevated levels returned to background rates within 6–8 years after harvesting. However, Caspersen (2006) examined experimental stands where trees were felled, but skidders did not remove timber. Thus, increases in PHM in operational stands are likely higher given that skidders are often the primary agents of residual tree damage and mortality during harvesting operations in a variety of managed forests (Lamson et al., 1985; Nichols et al., 1994; Thorpe et al., 2008). Published data from commercial selection-managed forests in Quebec offer mixed support for higher rates of PHM: assuming natural mortality rates of 1.5% year^{-1}, data extrapolated from Forget et al. (2007) suggested mortality increases of 0.4% over 10 years, while others have reported increases in mortality of 10.5–12.2% over 10 years (Bédard and Brassard, 2002).

Information on the causes of PHM mortality following selection harvests is even more limited. Previous work from other forest types and harvesting regimes has focused on windthrow as a main postharvest mortality agent (Ruel, 1995; Coates, 1997; Huggard et al., 1999; Ruel et al., 2001, 2003). Yet selection harvests, with their low removal rates, may result in different causes of mortality and these may change through time. Trees showing severe damage from felling and skidding operations are likely to die very quickly. In contrast, if harvesting does not kill trees immediately, those exposed to skidder activity and felling damage may be predisposed to higher long-term mortality risk due to fungal infections (Hesterberg and Ohman, 1963; Nichols et al., 1994; Mycroft, 2010) or reduced competitive status (Jones and Thomas, 2004; Bladon et al., 2008; Hartmann et al., 2009). Differences in causes of mortality could also lead to differences in the type and function of coarse wood (i.e., standing vs. downed) present on the landscape (Bladon et al., 2008), with implications for the availability of wildlife habitat (Holloway et al., 2007; Vanderwel et al., 2008, 2010).

This study was designed to elucidate patterns and causes of tree mortality following single-tree selection harvesting in Ontario's hardwood forests. We addressed three main questions: (1) What are the temporal patterns of postharvest tree mortality following selection harvesting? (2) What tree species and size classes are most susceptible to mortality following single-tree selection harvesting? and (3) What are the main types and causes of tree mortality following selection harvesting?

2. Methods

2.1. Field-based study

Field sampling was conducted at the Haliburton Forest and Wildlife Reserve (HF), a 25,000-ha privately owned forest in central Ontario, Canada (43° 13′ N, 78° 35′ W). Located within the Great Lakes-St. Lawrence forest region, the forest has been managed by selection harvesting for the past 40 years. Prior to this time, the forest was high-graded for *Pinus strobus* L. and *Betula alleghaniensis* Brit. (Mrosek et al., 2006). *Acer saccharum* Marsh. is the dominant species in the forest, comprising roughly 60% of the total basal area which ranges between $\sim$ 15-30m^{2}ha^{-1} on most upland sites (Domke et al., 2007). Other commercial hardwood species include: *Fagus grandifolia* Ehrh., *B. alleghaniensis*, *Prunus serotina* Ehrh., *Fraxinus americana* L., and *Quercus rubra* L. (Jones and Thomas, 2004).

Selection management in HF removes approximately 1/3 of the standing basal area every 20-25 years. All harvested blocks in the study were cut using conventional harvesting techniques common in the region (OMNR, 1998). Specifically, harvesting is designed to approximate a target size class distribution (q-ratio of 1.16), with trees directionally hand felled, topped, and delimbed using chainsaws. Tree-lengths were dragged up to 1 km to small landings with cable skidders. Because the silvicultural objective of the selection harvesting is to naturally regenerate shade-tolerant and certain mid-tolerant hardwoods (i.e. *B. alleghaniensis*, *P. serotina*, and *Q. rubra*), no deliberate understorey vegetation management or soil scarification prior to or immediately post harvest was done in any of the blocks. The layout of skid trails was typical of selection harvesting with main skid trails, approximately 3-5 m wide, spaced every 25-50m depending on local topography. Secondary and tertiary trails were located as needed to access trees marked for removal.

Since 1985, accurate records of cutblock locations have been maintained throughout HF making it possible to examine PHM using a chronosequence approach. Our study made use of a subset of sample plots established as part of a previous study designed to analyze postharvest tree growth and gap-closure rates (see Domke et al., 2007; Jones et al., 2009). Operational stands from seven harvest years were identified, spanning an 11-year chronosequence (Table 1). For each harvest year (except 2000), two to three distinct cutblocks were identified and located to ensure spatial interspersion of plots within a given harvest year. In all cutblocks, harvesting occurred during the summer, fall, and winter months. Removal rates in sampled plots ranged from 7.3-15.5 m^{2}ha^{-1} of the standing basal area (Domke et al., 2007). Within each cutblock, primary skid trails were located and transects extending the length of the skid trail were established. At 100-m intervals along the main transect, paired 20-m fixed radius plots were established with plot center points located at a 50 m perpendicular distance from transect lines. Although we attempted to resurvey all plots, we could not relocate five plots harvested in 1997, and one plot harvested in 1998 (Table 1). In total 134 inventory plots were surveyed, representing a 16.84 ha area of forest. All cutblocks harvested during or prior to 2003 were sampled June through August 2005, while cutblocks harvested in 2005 were sampled in August 2006.

Within each plot, all live trees $\geqslant$8 cm in diameter at 1.3 m aboveground (dbh) and cut stumps had been previously identified to species, measured, and mapped (Domke et al., 2007; Jones et al., 2009). Upon revisiting these plots, we located and identified all dead trees that were not intentionally felled (identified by the lack of a cut surface), measured diameter at 1.3 m from the base, and assigned a decay class category (consistent with Vanderwel et al., 2008). A detailed diagnostic examination of physical characteristics was then conducted to infer the main cause of mortality. Infer-

Table 1
Sample sizes, mean number of stems (ha^{-1}), and mean postharvest basal area (m^2 ha^{-1}) for all 20-m fixed radius plots measured in this study. Year harvested corresponds to the calendar year in which harvesting took place, years since harvest corresponds to the difference between sampling year and harvest year, and postharvest plot data are from Jones et al. (2009).

Year harvested	Years since harvest	Number plots sampled	Number of cutblocks	Mean number stems (ha^{-1})	Mean postharvest basal area (m^2 ha^{-1})
1994	11	20	2	466	17.47
1997	8	15	2	549	18.65
1998	7	19	3	534	19.83
2000	5	20	1	431	18.69
2002	3	20	2	394	17.97
2003	2	20	3	445	21.25
2005	1	20	2	499	19.60

ences of mortality causes were based on the "type" of stem breakage—(1) standing dead (snag), (2) tip-up, (3) stem-snap, (4) basal snap, or (5) skidder knockdown; hereafter referred to as "mortality types"—as well as decay class characteristics and physical symptoms visible on the stem. For each dead tree we also documented the condition of the crown (damaged/undamaged), large branches (presence/absence), fine branches (presence/absence), bark remnants on the bole (presence/absence), root plate (presence/absence), and the degree of wood firmness (subjective 1–5 scale). Finally, on each dead tree specific mortality symptoms were identified and recorded including presence of bark scars (size/position), fungal fruiting bodies (primary/secondary species), heart rot (percentage), frost cracks (size), fall direction (degrees from base to crown), and branch/crown damage.

Based on a thorough diagnostic assessment of each tree, a probable cause of mortality was inferred. The six observable causes of tree mortality identified were: (1) skidder damage, referring to mortality by stem-knockdown or severe abrasion by logging machinery, (2) felling damage, referring to mortality due to damage induced by nearby felled trees, (3) windthrow, (4) boring insect damage, (5) fungal infection (both above- and belowground), and (6) natural senescence, referring to a diagnosis by elimination in which the absence of explicit mortality agents or stem damage suggested mortality due to competition. Due to relatively small sample sizes in some of these categories, we pooled the mortality causes into three groups for analysis: (1) mechanical damage (i.e., skidder and felling damage), (2) biotic agents (i.e., fungal infection, natural senescence, and insect damage), and (3) windthrow. To ensure consistency in inferring mortality causes, all diagnoses were made by a single observer (A.R. Martin).

2.2. Data analysis – rates and time course of PHM

To ascertain rates of PHM through time, we used dendrochronological analysis to assign a year of mortality to each dead tree. A wood disc was taken from each dead tree, and ring widths were measured along two radii using WinDendro v. 2003b software (Regent Instruments, Quebec City, Quebec, Canada). Cross-dating was then performed with skeleton plots created using the 'dplR' package in R v. 2.10.1 (Bunn, 2008; R Foundation for Statistical Computing, Vienna, Austria). For all skeleton plot analyses, we compared dead tree chronologies to a site-specific master series derived from a previous study (Jones et al., 2009). For each tree, year of death was recorded as the year following the final year of diameter growth (Thorpe et al., 2008). Of the total 439 dead trees sampled we were able to crossdate 299 trees. For trees that could not be cross-dated we estimated year of death using decay class as a proxy, as informed by our dendrochronological analysis. Specifically, all cross-dated trees were first grouped by decay class, and we then calculated a median time since death of 2, 4, 8, 10, and 13 years for decay classes 1 through 5, respectively. For all crossdated trees, dendrochronology-based year of death determinations significantly predicted decay class-based year of death determina-

tions ($n = 299$, $P < 0.0001$, $r^2 = 0.401$ for a linear regression model forced through the origin), and the two data sets (i.e., dendro- vs. decay class-based year of death determinations) did not differ significantly (pair t-test: $t_{298} = 1.99$, $P = 0.06$). (In addition to the linear regression analysis, we conducted a mixed-effects modelling analysis that sought to account for species-specific differences in decay rates when predicting year of death, by including species identity as a random effect. The fit of the mixed-effects model was nearly identical to the simple linear regression model (Akaike's Information Criteria (AIC) value = 1460 and 1462.6, respectively; log-likelihood = -727.2 and -729.3, respectively; model slope = 0.52 ± 0.04 (S.E.) and 0.54 ± 0.04, respectively), suggesting a linear regression model based on species-pooled data was sufficient in predicting year of death from decay classes in our dataset.) All trees determined to have died prior to harvest ($n = 161$) were removed from the data set leaving a final sample size of 278 trees that died postharvest.

Using tree maps from each plot, PHM was quantified as a percent stem loss (stems ha^{-1}) and percentage basal area loss (m^2 ha^{-1}). We initially sought to model rates of PHM through time by employing a mixed-modeling approach that accounted for potential spatial autocorrelation among plots nested within cutblocks. However this was not possible since there was not complete replication of all cutblocks across the entire chronosequence, resulting in an overparameterized model that would not converge. We therefore proceeded with an analysis of PHM rates through time using least squares models (as suggested by Pinheiro and Bates, 2000). For this analysis we calculated mean PHM rates per cutblock, and PHM rates were examined as a function of time since harvest in years (where $n = 87$ cutblock-by-years-since-harvest data points). Rates of PHM through time were described using four explanatory models, which were then compared using AIC values. The first explanatory model was a linear regression model of the form:

$$\text{PHM} = a + b(t_{\text{ph}}) \tag{1}$$

where a is the intercept, and b represents the coefficient for time since harvest in years (t_{ph}). The second model was a linear regression model with a 2nd-order polynomial term of the form:

$$\text{PHM} = a + b(t_{\text{ph}}) + c(t_{\text{ph}}^2) \tag{2}$$

where a, b, and t_{ph} are as in Eq. (1) and c is the coefficient for the t_{ph}^2 term. The third model was a negative exponential model of the form:

$$\text{PHM} = a(t_{\text{ph}})^{-b} \tag{3}$$

where t_{ph} is as in Eq. (1), and a and b are constants fit with maximum likelihood, representing maximum mortality rate at one year postharvest, and rate of decline in tree mortality with time since harvest, respectively. (We also tested a three-parameter version of Eq. (3) of the form PHM = $a(t_{\text{ph}}^{-b}) + c$, where c represents the asymptotic background mortality rate. On both a basal area and stem basis, c was not significantly different than 0 and parameter fits within

1 standard error were negative (0.043 ± 0.683 (s.e.) and 0.0003 ± 0.585, respectively). Explanatory power of the three-parameter models was also identical to the two-parameter models; therefore here we present only the two-parameter model; Eq. (3)).

The fourth model was a unimodal fit of the form:

$$PHM = a * b^{(t_{ph}-c)^2} \qquad (4)$$

where t_{ph} is as in Eq. (1) and a, b, and c are constants fit with maximum likelihood. In Eq. (4), a represents the mean mortality rate, b controls the shape of unimodality, and c represents the year of peak tree mortality.

2.3. Data analysis – species and size class susceptibility

We initially attempted to model species-specific mortality rates by incorporating species terms in our predictive models (Eqs. (1)–(4)). However due to a low number of dead stems for most species in our dataset across the entire chronosequence, these analyses yielded little insight into species susceptibility to PHM. We therefore used log-linear models to examine which species and tree size classes were most susceptible to mortality following harvest. Prior to analysis, some species were grouped due to low sample sizes (where $n \leqslant 7$ dead stems). Specifically, *Acer pensylvanicum* L., *Acer rubrum* L., *Betula papyrifera* Marsh., *F. americana*, *Fraxinus pennsylvanica* Marshall, *Ostrya virginiana* (Mill.) K. Koch, *P. serotina*, and *Ulmus americana* L. were grouped into a "hardwood" classification, while *Thuja occidentalis* L. and *Picea rubens* Sarg. were placed into a "conifer" group. Tree size classes were based on tree dbh, as modified from the Ontario Ministry of Natural Resource's (OMNR) silviculture guide (OMNR, 1998): saplings (8–17 cm dbh), polewood (17.1–25 cm dbh), small sawlogs (25.1–35 cm dbh), and large sawlogs ($\geqslant$35.1 cm dbh). We used likelihood ratio tests (or G-tests) to determine if dead tree size- and species abundances differed significantly from those of live trees. Null expectations for frequencies were based on the same inventory plots used to survey tree mortality (Domke et al., 2007; Jones et al., 2009). For each size and species group, we also calculated the likelihood (or odds ratio) that a tree of a given size or size group would die following harvest. For these calculations, likelihood of mortality for a given size group or species was expressed relative to the entire pooled data set.

2.4. Data analysis – types and causes of PHM

To examine types and causes of PHM, all observations were pooled into size class groups and Chi-square analysis used to test
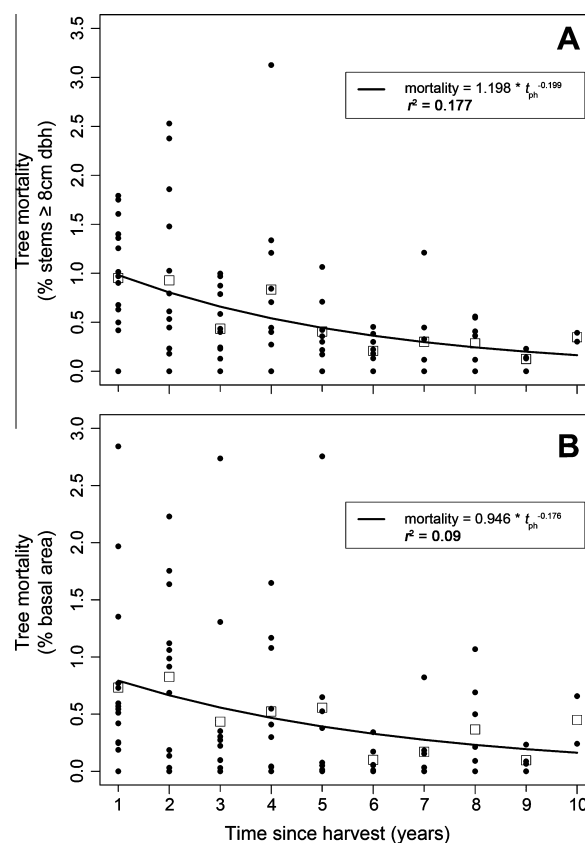

Fig. 1. Estimated tree mortality rate as a function of years since harvest ("t_{ph}") following single-tree selection harvesting in Haliburton Forest, central Ontario. Tree mortality rates are expressed as average mortality for each cutblock, on a percent stem basis (A) and percent basal area basis (B); $n = 87$ in both cases. Open squares represent mean mortality rates per year, and trend lines, equations, and coefficients of determination (r^2) represent the most parsimonious models predicting tree mortality through time (see Table 2).

if the prevalence of observed types and causes of mortality differed significantly from what would be expected by chance. Due to several expected frequencies that were low, Chi-square test statistics and associated P-values were calculated using Monte Carlo simulations with 2000 replicates. This analysis was not performed on a species basis, since dividing observations across eight species groups by five different mortality types or three different mortality causes led to several groups with no observations.

Table 2

Models predicting the rate of postharvest tree mortality as a function of time since harvest. Parameters and diagnostics of four models predicting postharvest tree mortality rates as a function of time since harvest, on both a per stem- and a basal area basis for trees $\geqslant$8 cm in diameter at breast height. Parameters and equations for all models are presented in Eqs. (1)–(4), and asterisks denote significance of individual parameters for each model ($^* = P < 0.05$, $^{**} = P < 0.01$, and $^{***} = P < 0.0001$). Highlighted in bold are the most parsimonious model fits based on model AIC values.

	Linear	Polynomial	Negative exponential	Unimodal
Percent stem basis				
a (±S.E.)	0.998 (0.119)***	1.17 (0.2)***	**1.198 (0.2)*****	0.913 (0.251)***
b (±S.E.)	−0.098 (0.024)***	−0.2 (0.098)*	**−0.199 (0.057)*****	0.972 (0.031)***
c (±S.E.)	NA	0.011 (0.01)	**NA**	0.2 (3.617)
Model r^2	0167	0.178	**0.177**	0.169
Model P	<0.0001	<0.0001	**NA**	NA
Model AIC	154.64	155.46	**153.58**	156.47
Percent basal area basis				
a (±S.E.)	0.808 (0.132)***	0.962 (0.223)***	**0.946 (0.21)*****	0.744 (027)**
b (±S.E.)	−0.074 (0.027)**	−0.165 (0.109)	**−0.176 (0.072)***	0.975 (0.038)***
c (±S.E.)	NA	0.009 (0.011)	**NA**	0.2 (5.2)
Model r^2	0.085	0.093	**0.091**	0.093
Model P	0.006	0.017	**NA**	NA
Model AIC	173.21	174.45	**172.65**	175.03

We also examined relationships among mortality types, mortality causes, and years since harvest. To do so we performed a backwards step-wise log-linear model fitting procedure on generalized linear models (GLM) with a Poisson error distribution. In this procedure, the full model predicted the frequency of mortality observations as a function of type, cause, and time since harvest (in years), as well as all interaction terms (two-way and three-way). Significance of individual predictors and interaction terms in competing GLMs was assessed through log-likelihood ratio tests.

3. Results

3.1. Postharvest mortality rates

Rates of PHM varied significantly as a function of time since harvest, and were best described by a negative exponential model (Table 2 and Fig. 1). On a percent stem basis, the negative exponential model explained 17.7% of the variation in tree mortality (Table 2 and Fig. 1A), but on a basal area basis it explained only 9.1% of the variation (Table 2 and Fig. 1B). Linear models (with and without quadratic terms) and unimodal models provided less strong predictions of PHM rates through time (Table 2). For both measures of PHM, the general pattern of tree mortality following selection harvesting was consistent: observed tree mortality peaked between one and two years postharvest, followed by a gradual reduction in PHM rates from three through five years postharvest, then continued to decline gradually from six through 10 years postharvest (Fig. 1).

On a per stem basis, observed PHM was greatest at one and two years postharvest, averaging 0.94 ± 0.14% (S.E.) declining between three through five years postharvest to 0.56 ± 0.11% on average (Fig. 1A). Beyond five years postharvest, tree mortality rates stabilized at 0.25 ± 0.05% on average (Fig. 1A). Mortality rates on a basal area basis showed similar patterns (Fig. 1B). At one and two years postharvest, observed PHM rates were 0.78 ± 0.14%, dropping to 0.54 ± 0.17% at three through five years postharvest, and stabilizing at 0.21 ± 0.05% beyond five years postharvest (Fig. 1B).

3.2. Species and size class susceptibility to postharvest mortality

Species composition of dead trees differed significantly from that of live trees ($G = 65.10$, df = 7, $P < 0.001$). On a per stem basis ($n = 128$), A. saccharum was the most commonly observed species constituting 46.0% of all dead trees (Table 3). However, when average mortality risks were compared, A. saccharum was one of the species least susceptible to PHM (mortality odds ratio = 0.76; Table 3). Similarly, F. grandifolia—the next most common species in the mortality data set (9.4% of dead trees, $n = 26$ dead trees)— was also one of the least susceptible to PHM (mortality odds ratio = 0.71; Table 3). All conifers were more susceptible than average to PHM (Table 3), as was the economically important timber species B. alleghaniensis (mortality odds ratios = 1.47; Table 3).

Patterns of tree mortality after harvest also showed strong size dependence, and the size distribution of dead trees differed significantly from that of live trees ($G = 23.13$, df = 3, $P < 0.001$). The largest number of dead trees was in the sapling size class (8–17 cm dbh), where 154 dead trees represented 55.4% of total PMH (Table 4). Sapling-sized trees were 1.3 times more likely than average to experience PHM (Table 4). Polewood-sized trees (17.1–25 cm dbh) represented 21.6% of dead trees (60 individuals) and were second-most susceptible to PHM (mortality odds ratio = 0.89; Table 4). Successively lower numbers of dead trees were found in the small sawlog (25.1–35 cm dbh, $n = 36$) and large sawlog ($\geqslant$ 35 cm dbh, $n = 28$) size classes (Table 4). Small and large sawlogs were also the least susceptible to PHM, with mortality likelihoods roughly half of the average values (mortality odds ratios = 0.68 and 0.67, respectively; Table 4).

3.3. Tree mortality types and causes

Across all size categories, standing dead trees (snags) were the most common mortality type observed, accounting for 110 of 278 (39.6%) dead trees (Fig. 2A). Tip-ups and stem snaps also accounted for large proportions of observed dead trees, constituting 54 (19.4%) and 61 (21.9%) of total dead trees, respectively (Fig. 2A). Basal snaps and knockdowns were the least common mortality types, constituting 33 (11.9%) and 20 (7.2%) of total dead tree observations, respectively (Fig. 2A). Skidder knockdowns were almost exclusively observed in the sapling size class (Fig. 2A). Mortality types across size categories differed significantly from a random expectation ($\chi^2 = 25.89$, $P = 0.01$; Fig. 2A).

With respect to mortality causes, mechanical damage from harvesting (i.e., skidder damage and tree damage due to tree felling) was the most commonly diagnosed cause of tree mortality accounting for 126 (45.3%) tree deaths (Fig. 2B). Biotic agents (fungal infection and senescence) accounted for an additional 90 (32.4%) tree deaths following harvesting, while windthrow accounted for 62 (22.3%) tree deaths (Fig. 2B). The observed distribution of mortality causes across size classes deviated significantly from a random expectation ($\chi^2 = 19.43$, $P = 0.003$; Fig. 2B). Mechanical damage was largely concentrated in the sapling and polewood size classes: of the 126 trees killed by skidding and felling damage, 64.3% were in the sapling size class while 21.4% were in the polewood size class. Comparatively few (14.3%) observed instances of mortality due to skidder or felling damage were observed in the small or large sawlog size classes (Fig. 2B).

The prevalence of observable causes of PHM was significantly related to the type of tree mortality observed, both of which varied

Table 3
Number and proportion of dead ($n = 278$) and live ($n = 7930$) trees observed across six temperate tree species and two generalized categories, from 134 forest inventory plots in Haliburton Forest. Composition of dead trees differed significantly compared to composition of live trees ($G = 65.10$, d.f. = 7, $P < 0.001$). Species are arranged according to the odds of experiencing mortality following harvest: mortality odds ratios >1 indicate species have a higher than average likelihood of experiencing mortality, while ratios < 1 indicate species have a lower than average likelihood of experiencing mortality.

Species	Live trees	Postharvest mortality	Mortality odds ratio
Fagus grandifolia	1046 (13.2%)	26 (9.4%)	0.71
Acer saccharum	4802 (60.6%)	128 (46.0%)	0.76
Hardwood spp.[*]	730 (9.2%)	32 (11.5%)	1.25
Tsuga canadensis	455 (5.7%)	23 (8.3%)	1.44
Betula alleghaniensis	372 (4.7%)	19 (6.8%)	1.46
Abies balsamea	342 (4.3%)	25 (9.0%)	2.09
Picea glauca	156 (2.0%)	16 (5.8%)	2.93
Softwood spp.[**]	27 (0.3%)	9 (3.2%)	9.51

[*] Includes *A. pensylvanicum, A. rubrum, B. papyrifera, F. americana, F. pennsylvanica, O. virginiana, P. serotina,* and *U. Americana.*
[**] Includes *T. occidentalis* and *P. rubens.*

Table 4

Number and proportion of dead ($n = 278$) and live ($n = 7930$) trees across four tree size classes from 134 forest inventory plots. Tree size classes are modified from Ontario Ministry of Natural Resources guidelines (OMNR, 1998). Size class distribution of dead trees differed significantly compared to that of live trees ($G = 23.13$, d.f. = 3, $P < 0.001$). Mortality odds ratios >1 indicate size classes with a higher than average likelihood of experiencing mortality, while ratios <1 indicate size classes with a lower than average likelihood of experiencing mortality.

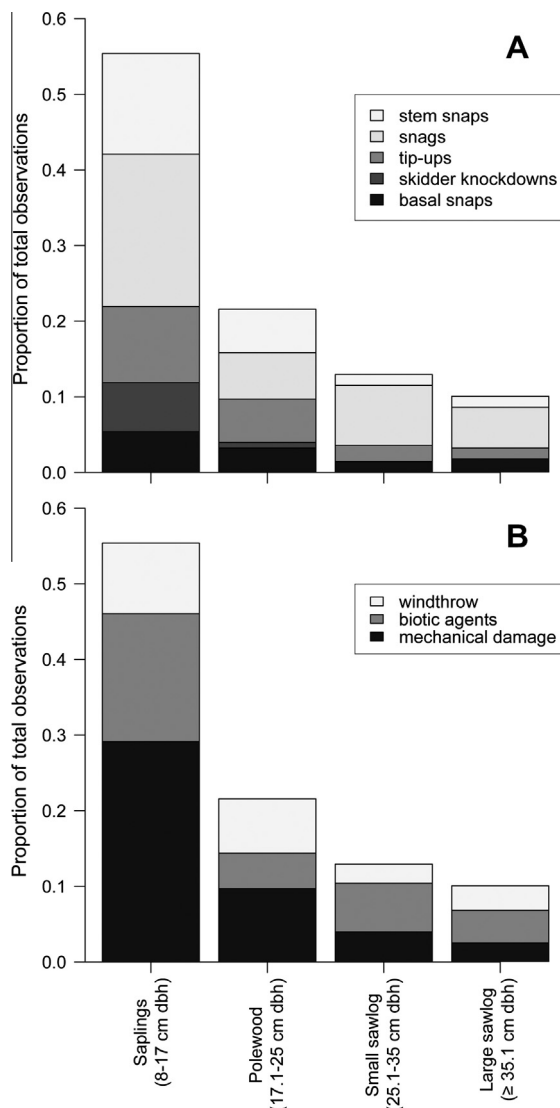| Size class	Live trees	Postharvest mortality	Mortality odds ratio
Saplings (8–17 cm dbh)	3292 (41.5%)	154 (55.4%)	1.33
Polewood (17.1–25 cm dbh)	1932 (24.4%)	60 (21.6%)	0.89
Small sawlogs (25.1–35 cm dbh)	1514 (19.1%)	36 (13.0%)	0.68
Large sawlogs ($\geqslant$35.1 cm dbh)	1192 (15.0%)	28 (10.1%)	0.67

Fig. 2. Proportions of observed tree mortality by types (A) and causes (B) following single-tree selection harvesting in Haliburton Forest, central Ontario, in the sapling ($n = 154$), polewood ($n = 60$), small sawlog ($n = 36$), and large sawlog ($n = 28$) size classes, across the entire data set ($n = 278$). Number of observations found in each type-by-size group differed significantly from a random expectation ($\chi^2 = 25.89$, $P = 0.01$), as did the number of trees observed in each cause-by-size group ($\chi^2 = 19.43$, $P = 0.003$).

systematically with time since harvest (Table 5 and Fig. 3). GLM analysis found that type-by-year-since-harvest (dev. = 82.3, df = 24, $P < 0.0001$), cause-by-year-since-harvest (dev. = 77.3, df = 12, $P < 0.0001$), and cause-by-type (dev. = 89.9, df = 8, $P < 0.0001$) interaction terms were all significant explanatory variables of mortality frequencies (Table 5). Of the interaction terms in the model, inclusion of the cause-by-type interaction term resulted

in the largest reduction in deviance from observed frequencies (Table 5). This trend was supported by qualitative assessment of mortality proportions through time: in the first year postharvest when skidding and felling operations killed 100% of newly dead trees, 89.1% of dead trees were found as downed wood (i.e., skidder knockdowns or tipups; Fig. 3). However, by three years after harvest senescence and above- and belowground fungal infection became more prominent (Fig. 3B), with a progressively larger proportion of dead stems found standing (snags) or partially standing (stem snaps; Fig. 3A). Backwards step-wise modeling analysis confirmed significant covariation among mortality type, cause, and time since harvest. A log-linear model including these three variables as well as all two-way interactions was the strongest in explaining observed mortality frequencies (AIC = 156.2 vs. AIC = 210.0 in the full model). Removal of other explanatory variables or interaction terms did not reduce model AIC values (data not shown).

4. Discussion

4.1. Rates of postharvest mortality

Our data indicates that following single-tree selection harvesting a small pulse of mortality can be expected within standard harvesting cycles (Fig. 1 and Table 2). Although the observed rates of PHM following selection harvests in HF are much smaller than those reported in other managed systems, our results contribute to growing evidence suggesting significant changes in tree mortality occur through time as a result of harvesting (Coates, 1997; Ruel et al., 2001, 2003; Caspersen, 2006; Bladon et al., 2008; Thorpe et al., 2008; Cimon-Morin et al., 2010). While some authors have suggested that PHM rates may persist or increase through time (Ruel et al., 2001, 2003), here we found the highest PHM rates occurred within two years postharvest followed by an additional three-year period of further decline (Fig. 1).

Our data suggested that cumulative losses due to PHM in selection-managed forests are small over 20-year rotations, particularly when compared to nearby unmanaged stands (OMNR, 1998). Expressing our modeled estimate of tree mortality on a basal area basis (Table 2 and Fig. 1B) indicated that over 20 years, cumulative mortality in HF following selection harvesting is 13.2%. Compared to average rates of mortality of 0.95% year^{-1} observed in a 13.5-ha unmanaged inventory plot in HF (0.78–1.18%, 95% C.I.; cumulatively 19.2% over a 20-year harvest interval on average; S.C. Thomas, unpublished data), our modeled estimates represent a decrease in mortality of 6.0% over 20-year harvesting cycles. These rates of tree mortality are substantially lower than PHM rates observed in other commercial and experimental forests. Specifically, increases in mortality of 6.4% on average at 16–22 years postharvest were reported in selection cuts in central Ontario (Morneault et al., 2011), while increases of 0.2–33% were reported following experimental selection harvests in which trees were felled but not skidded (Caspersen, 2006).

Our data is similar to other studies in finding that forest management may act to reduce tree mortality rates compared to that

Table 5

Parameters from a generalized linear model predicting frequency of tree mortality across different causes and types of mortality, and years since harvest, as well as all two-way and three-way interaction terms. The null model represents a prediction that observed frequencies across all type-cause-year since harvest combinations are equal. Significant predictors (highlighted in bold) represent those that when added to the model sequentially, led to a significant reduction in deviance from the observed frequencies (based on a likelihood ratio χ^2 test). The model incorporating all predictors except the year-by-cause-by-type interaction was the most parsimonious explanation of observed frequencies based on step-wise log-linear model analysis (see Section 3 for details).

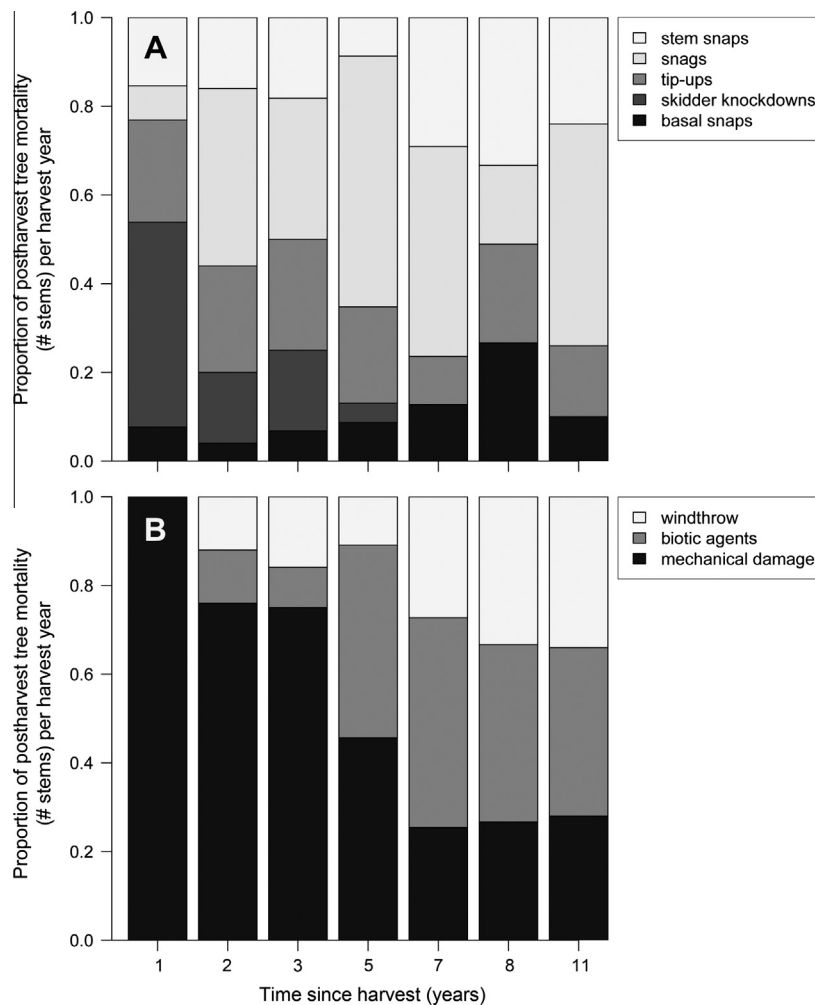| Predictors variables	df	Deviance	Residual df	Residual deviance	P value
Null model	–	–	104	437.31	–
Year	**6**	**40.453**	**98**	**396.85**	**<0.001**
Cause	**2**	**22.345**	**96**	**374.51**	**<0.001**
Type	**4**	**82.931**	**92**	**291.58**	**<0.001**
Year * cause	**12**	**77.256**	**80**	**214.32**	**<0.001**
Year * type	**24**	**82.274**	**56**	**132.05**	**<0.001**
Cause * type	**8**	**89.858**	**48**	**42.19**	**<0.001**
Year * cause * type	48	42.188	0	0	0.7089

Fig. 3. Proportions of observed tree mortality by types (A) and causes (B) following single-tree selection harvesting in Haliburton Forest, central Ontario. Sample sizes of observed dead stems by plots, grouped across the 10-year postharvest chronosequence were as follows: 1 (n = 13), 2 (n = 25), 3 (n = 44), 5 (n = 46), 7 (n = 55), 8 (n = 45), and 11 (n = 50); (n = 238 for entire data set). Types and causes of mortality were significantly associated with time since harvest (Table 5).

in unmanaged stands (Bédard and Majcen, 2001; Caspersen, 2006; Forget et al., 2007; Thorpe et al., 2008). In our data set, modeled tree mortality estimates are stable at ~0.55–0.7% year^{-1} from five to 20 years postharvest: compared to mortality in unmanaged stands at HF those values are below average (0.96% year^{-1}) and only approach lower 95% confidence bounds (0.78% year^{-1}; S.C. Thomas, unpublished data). Across longer time frames, it could be hypothesized that these low observed and modeled mortality rates are in part the net result of forest management practices. In selection harvesting, stressed and damaged trees that would be

likely to suffer natural mortality are preferentially removed. This could act to preempt tree mortality events that would occur naturally in a temporally dispersed pattern, instead concentrating them at the time of harvest. Also, our observed low mortality rates beyond five years postharvest are very similar to rates found in northern hardwood forests when crown shading was low (Caspersen et al., 2011). In our sites, low crown shading in the upper canopy is prevalent following harvests and can persist for 20 years, particularly on more heavily harvested sites (Domke et al., 2007). Since large sections of HF (including sites where our

plots are located) are now undergoing their second or third stand entry (Jones and Thomas, 2004), our overall observed low mortality rates may reflect longer-term management effects on tree mortality.

4.2. Species differences in PHM susceptibility

Recruitment of mid-successional species, such as *B. alleghaniensis*, is an important management goal in northern hardwood forests, yet it is commonly recognized that during the last century these species were being replaced by shade-tolerant species, most notably *A. saccharum* (Leadbitter et al., 2002; Leak and Sendak, 2002; Schuler, 2004; Neuendorff et al., 2007). This compositional shift is assumed to be precipitated in part by selection harvesting, with studies pointing to multiple contributing mechanisms including (1) rapid postharvest gap closure that limits mid-tolerant recruitment (Beaudet and Messier, 2002; Crow et al., 2002; Domke et al., 2007), (2) removal of large senescing canopy trees leading to reduced understorey light availability (Nock et al., 2008), and (3) more pronounced positive postharvest growth responses of shade-tolerant species (Wiser et al., 2005; Jones et al., 2009).

Our results further suggest that species differences in susceptibility to PHM contribute to shifts in species composition. Compared to other studies that employ long-term serial measurements (cf. Caspersen, 2006), one limitation of our study was the inability to model species-specific mortality rates through time due to low numbers of dead tree observations for several species across the entire chronosequence. However our results do show that *A. saccharum* was one of the species least susceptible to PHM, with only *F. grandifolia* being less susceptible (Table 3). In comparison *B. alleghaniensis*, a mid-tolerant hardwood species (Niinemets and Valladares, 2006), was more susceptible than average to PHM (Table 3). Interestingly, conifer species, namely *Picea glauca* (Moench) Voss and *Abies balsamea* (L.) Mill. deviate from this pattern as shade-tolerant species that were particularly susceptible to PHM (Table 3). In the case of *A. balsamea*, high susceptibility may largely be attributed to operational considerations, since it is identified as the species to be intentionally knocked down by skidders when stand access considerations demand. Additionally, both *A. balsamea* and *P. glauca* are particularly susceptible to mortality due to root rot fungus (i.e. *Armillaria* spp.; Gerlach et al., 1997). Disregarding these two species, the relationship between shade tolerance and susceptibility to PHM could be explained as a function of species' differences in above- and belowground wood characteristics. Shade-tolerant species generally have denser wood (Chave et al., 2009) and greater concentrations of non-structural carbohydrate storage compounds in woody tissues (Kobe, 1997). These characteristics are in turn correlated with a greater ability to regenerate lost or damaged photosynthetic tissues (Landhausser and Lieffers, 2002; Kabeya and Sakai, 2005), close bark wounds (Wargo, 1977), and, in some species, compartmentalize fungal infections to prevent xylem decay (Yu et al., 2003; Romero and Bolker, 2008; Romero et al., 2009). Slow-growing species are also associated with greater fine root diameter and lower root length: root biomass ratios, which could confer greater resistance to belowground harvesting damage (Comas and Eissenstat, 2004). Direct tests of wood and root traits as predictors of logging damage resistance and resilience could provide a mechanistic understanding of species' differences in PHM susceptibility.

4.3. Size-dependence of PHM susceptibility

In absolute terms, tree mortality in our study was concentrated in the sapling and polewood size classes (Fig. 2), and these size classes were more susceptible to PHM than the larger size classes (Table 4). These results are consistent with several studies examining postharvest damage and mortality in hardwood forests

(Lamson et al., 1985; Cline et al., 1991; Nichols et al., 1994; Seablom and Reed, 2005; Caspersen, 2006). Smaller trees are more likely to be damaged during harvesting due to the choices of machine operators, as they represent less immediate losses of merchantable timber. However, given that large proportions of sapling and polewood mortality were found as standing dead trees (Fig. 2), size-dependent differences in tree physiology and anatomy likely also influence resistance or resilience to harvesting damage. Potential mechanisms could include size-dependent increases in bark thickness (Hengst and Dawson, 1994) or resprouting potential (Morisset et al., 2012), or ontogenetic changes in leaf-level physiology (Thomas, 2010). Research on larger *A. saccharum* trees (⩾19.1 cm dbh) showed that belowground harvesting damage (soil compaction and root damage) did not affect postharvest growth (Hartmann et al., 2008). Yet saplings and pole-sized trees may be more influenced by harvesting damage if they have shallower rooting profiles.

Excessive damage to sapling- or pole-sized stems will certainly influence future tree size class distributions (Nyland, 1998), with implications for the composition and yield of future harvests. Since these effects are inherently long-term, we suggest that parameterizing forest simulation models (e.g., SORTIE, FVS) using our data is a tractable way to evaluate future consequences of size-dependent PHM susceptibility on stand structure and dynamics. Similar modeling work has been done following retention harvests in Ontario's boreal forests (Thorpe et al., 2010), but to our knowledge this has not been done for any selection-managed hardwood forest.

4.4. Types and causes of PHM through time

A critical goal of sustainable forest management is the maintenance of coarse woody debris as a structural feature in managed stands (Lindenmayer et al., 2006), and our data suggests that elevated PHM contributes to coarse woody debris stocks in the short term. However, the contribution of PHM to different coarse woody debris pools is time-dependent: the proportions of different types of coarse wood (i.e., standing vs. downed) changed significantly with time since harvest, which were in turn correlated with changes in mortality causes through time (Table 5 and Fig. 3). Direct harvest-related damage was the main cause of mortality within the first three years postharvest, leading to most stems being observed as downed woody debris (Fig. 3 and Table 5). Our data also suggested harvest damage results in an increase in snags (Fig. 3). At ⩾5 years postharvest, on average 43.4% of all dead trees were observed as snags (this increased to 67.4% when stem snaps were included), which was qualitatively associated with an increase in biotic causes (i.e., fungal infection and senescence) as the diagnosed reason for mortality (Fig. 3). Although >60% of snags are often removed during harvesting for safety reasons (Holloway et al., 2007), greater proportional recruitment of snags through time may in part compensate for these losses.

4.5. Conclusion

Our study contributes to a growing body of literature examining the consequences of structural retention harvesting in Canada's forests. Information on PHM rates, causes, and consequences is critical to objectively evaluating the success or failure of management systems using partial stand harvests. Despite the proliferation of methods and standards for pre- and postharvest monitoring, data availability on stand responses to harvesting varies widely across forest management units (e.g. Hickey et al., 2005) or is lacking (e.g. Boutin et al., 2009) in Canada and elsewhere. As one of the first evaluations of tree mortality rates in eastern North America's commercial selection-managed hardwood forests, the present study provides data useful for objectively evaluating the

effects of harvesting activity, informing potential changes to harvesting prescriptions by identifying trees that are notably susceptible to harvesting damage, and parameterizing models to evaluate the long-term effects of management practices on forest structure and function.

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